The evolution and subsequent classification of the Phasmatodea.

Robert Lind, 1 Tolliday Close, Wivenhoe, Colchester, Essex, CO7 9SL, U.K.

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Millions of years of evolution by natural selection have given us what today we classify as the order Phasmatodea. At first glance the degree of sophistication seen in these insects is impressive, but one must remember that evolution is an entirely "blind" process with no goals and is still continuing. The evolutionary path travelled by the Phasmatodea is responsible for the way in which the order, and its subsequent classification within the class Insecta, are currently arranged. The correct classification of species within genera, families and orders should reflect evolutionary branching from common ancestors. Although tracing the one true evolutionary route to the present day may at first seem straight-forward, in fact it is near impossible and relies greatly on interpretation of data from two sources. The first source of data available is the fossil record. Much of the work performed so far using the fossil record has centred on placing the order correctly amongst the other orders of insects. Secondly, phasmids alive today have provided the classification scheme within the order. This is achieved by examination of morphological characteristics of the phasmids alive today for comparison with other phasmids which provides relationships of similarities between phasmids which can be interpreted as their degree of relatedness. The method assumes that a high similarity of characteristics is likely to represent closeness of divergence. This method can also be performed with representatives from other insect orders to try and locate the order within class insecta amongst the other orders.

The first step in classifying the order is to put it in its correct place amongst the other orders of insects, the second is to attempt to sort out the order itself into smaller subdivisions of families and finally genera. Both living relatives and the fossil record have been used to place the Phasmatodea amongst the other orders of insect. However, as stressed earlier these methods rely greatly on the data provided for the interpretation, and may be the reason why these two methods have given slightly different results.

Let us first consider what information the fossil record can provide in classifying the Phasmatodea. As insect bodies are made of soft material they require a particular set of circumstances to be fossilised, such fossils are therefore rare. One such set of conditions results if the insect is caught in tree resin which, over millions of years, turns to amber. Such preserved insects that resemble phasmids have been found and have even been named, such as *Pseudoperia lineata* (Pictet & Hagen). This species is thought to have been relatively common and has been found as nymphs of various sizes up to 30mm within baltic amber. Another fossil of an insect wing dating back to the Cretaceous period has been put forward as belonging to a phasmid (Birket-Smith, 1981), although evidence for this fossil is based entirely on the wing venation patterns and is somewhat doubtful.

The fossil record is only of use to provide fundamental evolutionary steps such as the branching from a common ancestor into what is now separate orders. Using this kind of information it is possible to attempt to piece together links between unlikely relatives. For instance the order Dictyoptera contains the cockroaches and mantids, which today appear very different from one another. However they share a common ancestor and so are assigned to the same order. Using this type of palaeontological detective work it has been suggested by Hennig (1981) that the order Phasmatodea branched off during the Permian from a common ancestor known as *Tcholmanvissia*. The other branch leading from *Tcholmanvissia* lead to the Caelifera, a suborder of Orthoptera. The branch that led to *Tcholmanvissia* originated from an ancestor known as *Oedischia* which led also to the Ensifera, the other sub order of Orthoptera. So in fact perhaps the suborder Caelifera is more closely related to the Phasmatodea than to the suborder Ensifera (Figure 1).

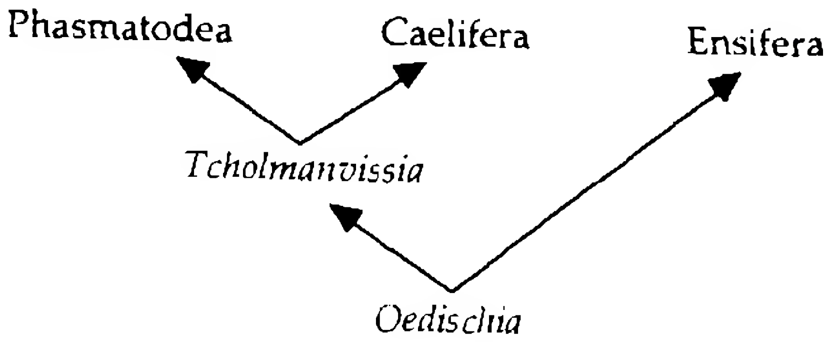

Figure 1. Possible evolutionary path of the Phasmatodea, as suggested by Hennig.

Living phasmids have also been used for the classification of the order within class Insecta and more importantly for closely related species and genera. Choosing the correct morphological feature to compare is important. For example body length is not good as this is a quantitative measure and is plastic in nature.

Discrete features are much better for this purpose such as the number of tarsi on the feet or wing venation patterns. By comparing features such as these an estimation of the degree of the evolutionary relationship can be obtained (Kamp, 1973). Firstly an attempt was made to put the order in its place amongst the other orders using various insect species which were compared with the Phasmatodea, whose representative was *Anisomorpha* sp. The degrees of similarity are computed and results used to produce a dendrogram showing the relationships between subjects. The dendrogram is a diagram which shows only current phenotypic relationships. Any attempt to read the branching as an evolutionary tree depends upon the assumption of equal evolutionary rates. One must take care with such analysis and realise that it is not straight forward to suggest that if features are very similar then those subjects are closely related, and similarly that markedly different subjects have only distant relationships. It depends upon the speed of the "evolutionary clock" as to how fast or slowly species diverge from one another. Species do not however only diverge they can also converge in a process of convergent evolution which can cause problems in this type of analysis.

It has already been put forward that natural selection has shaped the way in which the order appears today. But what is exactly meant by evolution by natural selection? In the vast majority of cases within the Phasmatodea the escape from predators involves mimicry, principally of plants upon which they live. The majority of predators of phasmids locate their prey mainly by sight and will therefore prey upon less camouflaged individuals in a population. It should be remembered that within a population of phasmids there is variation in the degree of mimicry, one has only to think of the coloration differences within a culture as well as the slight morphological differences. Those better camouflaged individuals manage to escape predation and go on to reproduce and pass on their characteristics, if they are determined genetically, to the next generation. This is what is meant by natural selection. However as the phasmid gets progressively better at camouflaging itself then this in turn puts a selection pressure on the predator population to select individuals that are better at being able to locate prey. This "arms race" between the predator and the prey has today given phasmids with incredible resemblance to plants and predators, such as birds, with incredible eyesight to spot them.

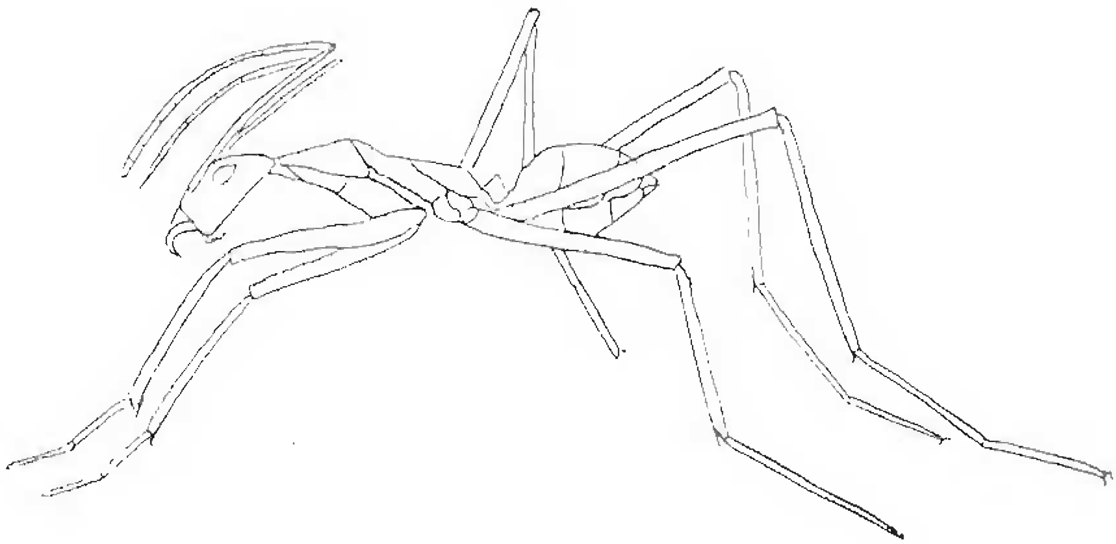

Figure 2. The ant *Leptomyrmex* sp.

It was mentioned earlier that phasmids resembled plant parts, but some have evolved to resemble, not plants, but other animals. An example of mimicry of other animals has been suggested by Key (1970) between first instar *Extatosoma tiaratum* and the foraging ant genus *Leptomyrmex* (Figure 2). The newly hatched *Extatosoma tiaratum* finds itself on the ground and needs to locate itself quickly into foliage, and mimicry of plants at this stage is not particularly helpful. However also running around on the ground are ants, the genus *Leptomyrmex* being one of them. The two insects share the same coloration and behaviour although they are not at all closely related. In fact this is an example of mimicry on the part of the *Extatosoma* which, over time, has had a selection pressure on it to select those individuals that look more ant like and therefore more likely to survive. Mimicry of the ant has presumably given it protection from predators during this vulnèrable life stage until it can find the safety of foliage.

References

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Editor's note

Readers may recall a recent paper by Hughes & Westoby (1992: Capitula on stick insect eggs and elaiosomes on seeds: convergent adaptations for burial by ants. *Functional Ecology*, 6: 642-648.) concerning the collection of seeds and phasmid eggs by ants. The mimicry of *Leptomyrmex* sp. by *Extatosoma tiaratum* would be particularly useful if *Leptomyrmex* collected *E. tiaratum* eggs which then hatched in the nest. However, as far as I am aware, no one has produced any evidence of this.